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Geographic variation of *Arvicanthis* (Rodentia, Muridae) in the Nile Valley

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Abstract

The size and shape differences in the skulls of nine populations of the rodents *Arvicanthis* along the Nile Valley (Egypt and Sudan) and one from Yemen were analysed. A three dimensional (x, y and z) landmark approach (Procrustes analysis) was used to study morphometric variation in these populations, in an attempt to evaluate differences between *A. niloticus* and *A. testicularis* and patterns of geographic variation. Size and shape differences were correlated to "ecogeographic" parameters (latitude, longitude, rainfall, temperature). Morphometric variation suggests that the two taxa have diversified in this area, and that variation reflects adaptation to current conditions. However, Partial Least Squares analysis showed that patterns of size and shape changes are different across species which suggests an independent evolutionary history.

Key words: *Arvicanthis*, geographic variation, geometric morphometrics

Introduction

Arvicanthis is a diurnal African rodent widespread in Egypt, Sudan, West, Central, East, and the Horn of Africa. It occurs in a great variety of habitats from sub-Saharan regions to Afroalpine moorlands, including croplands. However, the taxonomy of the genus is still provisional, as reflected by partial disagreements in the two most recent check lists of mammalian species (Corbet and Hill 1991; Musser and Carleton 1993).

Among the controversies, there is one which concerns the species occurring along the Nile Valley, from Egypt to Sudan and northern Ethiopia. According to Delany (1971), two species, *A. niloticus* and *A. testicularis*, occur in this area (the latter being considered synonymous to *A. dembeensis* by Corbet and Hill 1991, and synonymous to *A. niloticus* by Musser and Carleton 1993, who, however, include also *A. dembeensis* in this species). In a recent study, Philippi (1994) investigated cytogenetics and albumin and transferrin electrophoretic patterns in some animals from Cairo and Khartoum, and concluded that there are no differences and that individuals can reproduce. Furthermore, Philippi (1994) suggested that, although populations can be distinguished through a multivariate evaluation of skull linear measurements, this does not prove the occurrence of different species. However, patterns of geographic variation were not investigated and this may be important in assessing systematic relationships.

The aim of this study was to investigate the morphological variation in the form of the skull from populations of *Arvicanthis* along the Nile Valley, in an attempt to eventually distinguish between *A. niloticus* and *A. testicularis* and to explore patterns of geographic variation.

Rather than using traditional multivariate morphometrics, a landmark base approach, the core of geometric morphometrics (Bookstein 1991), was used. The new method of geometric morphometrics allows the recovery of the geometric properties of the skull in a Cartesian space, because morphological features are recorded as x, y and z co-ordinates. The 3-dimensional structure of the skull is thus preserved. This is advantageous because when using linear measurements typical of traditional morphometrics the 3-dimensional structure is lost. Moreover, three dimensional co-ordinates can be used for the statistical estimate of size and shape differences (after proper scaling, translation and rotation) as well as for their graphical visualisation (see, for a review, Rohlf and Marcus 1993; and Marcus and Corti 1996).

Material and methods

A total of 103 specimens from three populations in Egypt (Cairo, Asyut, and Aswan), six from Sudan (Merowe, Khartoum, Blue Nile, Kaka, Yuba, and Darfur) and one from Yemen (Lahej) were examined (Fig. 1; Tab. 1). Museum labels were used for species identification, and hereafter the names *A. testicularis* and *A. niloticus* will be used. The specimens of *A. niloticus* are from Egypt and Yemen and from the Blue Nile in Sudan; *A. testicularis* are all from Sudan. Individuals of *A. niloticus* and *A. testicularis* from the Khartoum area will be referred, respectively, as Khartoum(N) and Khartoum(T).

Specimens come from the collections of the British Museum of Natural History (London) and the Museo di Anatomia Comparata, Università di Roma 'La Sapienza'.

Four age classes were determined on the basis of molar tooth-wear, according to the amount of dentine exposure (Delany 1971).

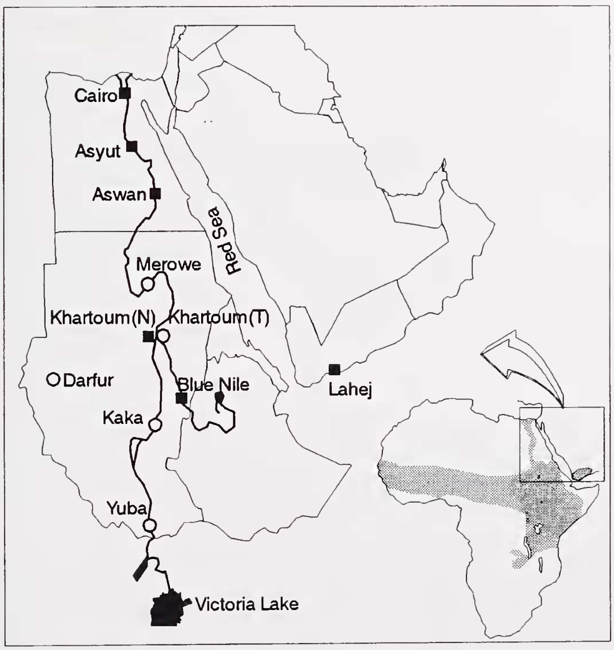

Fig. 1. Geographic location of the populations studied. Filled squares: *A. niloticus*; open circles: *A. testicularis*. The inset shows the approximate range of the genus *Arvicanthis*.

Table 1. Species, populations, geographic location, number of males and females (M/F), and the "ecogeographic" parameters recorded. MAT: Mean Annual Temperature; MJT: Mean July Temperature; MJaT: Mean January Temperature. MAR: Mean Annual Rainfall; MJR: Mean July Rainfall; MJaR: Mean January Rainfall (rainfall in mm). Dry: number of dry days during the year; Semi-dry: number of semi-dry days during the year; Humid: number of humid days during the year.

Species	Population	Latitude	Longitude	M/F	MAT	MJT	MJaT	MAR	MJR	MJaR	Dry	Semi-dry	Humid
A. niloticus	Asyut	27°03′N	31°01′E	3/5	22.9	30.0	13.5	0	0	0	365	0	0
	Aswan	24°02′N	32°53′E	2/4	26.9	34.0	16.7	1	0	0	365	0	0
	Blue Nile	11°47′N	34°23′E	8/8	28.1	31.7	26.0	736	384	0	242	80	43
	Cairo	30°03′N	31°13′E	7/8	20.5	34.7	12.2	19	0	11	365	0	0
	Khartoum	15°36′N	32°33′E	3/4	29.7	34.3	23.8	158	123	0	365	0	0
	Lahej	13°10′N	45°00′E	4/3	27.6	31.2	24.1	62	23	2	365	0	0
A. testicularis	Darfur	13°27′N	25°20′E	7/5	25.7	30.5	20.0	283	215	0	315	36	14
	Kaka	11°45′N	32°47′E	7/3	27.5	31.2	24.3	528	272	0	259	69	37
	Khartoum	15°36′N	32°33′E	4/5	29.7	34.3	23.8	158	123	0	365	0	0
	Merowe	19°10′N	29°20′E	3/0	27.6	34.1	30.9	21	6	0	365	0	0
	Yuba	04°52′N	31°36′E	7/3	27.4	25.4	28.1	971	271	12	150	123	92

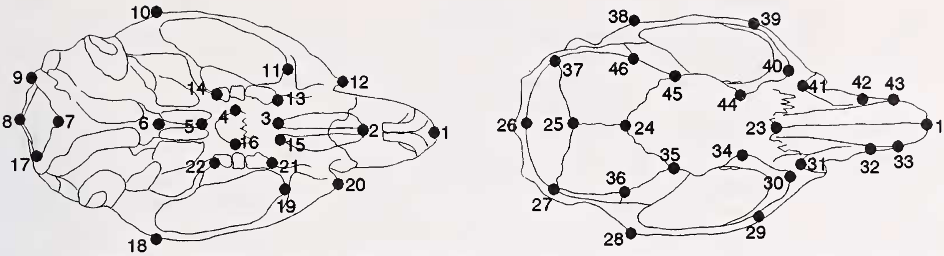

Fig. 2. The 46 landmarks collected as x, y, and z coordinates on the skull (shown from the dorsal and ventral view).

Images of the skull were obtained with a Sony CCD-F555E video-camera with a 10× zoom lens. The images were digitized through the VISIONplus-AT board (Imaging Technology Inc.). X and y co-ordinates were collected using the MTV software (Uptegraff 1990–1993). To reconstruct three dimensional x, y, z co-ordinates from two dimensional images, the images were collected at 0°, 45°, 120°, 180°, 240°, and 315° degrees, and three dimensional co-ordinates were then obtained from two dimensional co-ordinates by translation and rotation, resulting in 46 x, y, z landmarks (Fig. 2).

To avoid the effect of lateral asymmetry, the two sides of the skull were averaged and the y co-ordinates of landmarks located on the sagittal plane were set to zero. The averaged configurations were then reflected to obtain the complete representation of the skull.

The two components of the form, i. e. size and shape, were partitioned as follows. The centroid size, i. e. the square root ot the sum of the square of the distances of each landmark from the centroid (Bookstein 1991), was computed to best calculate the size of each specimen. Size differences between populations were tested by ANOVA (unbalanced design) and shown through box plot, excluding age class one.

Specimens were superimposed (translated, rotated, and scaled) over the consensus form through the Generalized Least Square Procrustes procedure (GLS; Rohlf and Slice 1990), using the GRF-nd program (Slice 1993). These new co-ordinates of the aligned specimens are standardised to unitarian centroid size; thus, they represent the shape component of the form and they were used for all statistical analyses of shape.

Sexual dimorphism in shape was estimated through MANOVAs (unbalanced design) for each landmark (x, y, z co-ordinates).

Eigenvalues and eigenvectors from the variance-covariance matrix of the new co-ordinates were extracted and used to investigate trends in variation. Shape changes associated to each eigenvector were visualised as displacements from the consensus using the program GRF-nd. This allows to relate the ordination of each principal component to a typical associated shape change.

A Model II ANOVA was performed following the Leamy (1983) procedure to test whether sex, age, and their interaction affect the principal components used to describe shape variation between species and populations. To visualise morphometric similarities between populations, a Minimum Spanning Tree was calculated from the Procrustes distances (Bookstein 1991).

As there is a clinal climatic variation along the Nile river with a dramatic aridity increase from Cairo to Merowe, the following geographic and climatological parameters were recorded (hereafter referred as "ecogeographic"): latitude and longitude; mean annual raintall (MAR), mean January rainfall (MJaR), mean July rainfall (MJR), all in mm; mean annual temperature (MAT), mean January temperature (MJaT), mean July temperature (MJT); number of dry, semi-dry, and rainy days during the year (Tab. 1). These data were collected from the F. A. O. Economist Intelligence Unit (1995).

Centroid size and shape for each individual were related to these parameters through multiple regression and Partial Least Square (PLS; Streissguth et al. 1993), respectively. PLS is a multivariate technique based on the singular value decomposition of the correlation matrix between two blocks or arrays of variables ("left" and "right" blocks), so that the predictive interrelations between the two are summarised by two sets of latent vectors, one for each block. In this case, the left block was represented by population scores on the first three principal components, and the right block by the geographic and climatic parameters.

The box plots were obtained using the STATISTICA program (1993), the Minimum Spanning Tree and the PLS with the NTSYS-PC program (Rohlf 1993) and all other statistical analysis using the SAS statistical package (1993).

Results

Analysis of size differences

Size differences between populations are significant ($F = 30.68$, $P < 0.001$). These differences are represented by the box plot in figure 3. In general, *A. niloticus* is larger than *A. testicularis.* Individuals of Asyut are significantly larger than other populations (with the exception of Blue Nile and Cairo), and the population of Lahej from Yemen is significantly different from the smallest populations, i. e. Merowe and Darfur.

The multiple regression of centroid size on geographic and climatic parameters suggested a general trend in size decrease from North to South. The vector representing the "ecogeographic" parameters is highly correlated with latitude ($r = 0.97$) and it is negatively correlated with the mean annual rainfall and mean annual temperature (respectively $r = -0.80$ and $r = -0.97$); the correlation with centroid size is 0.40 which indicates an overall significance of $P < 0.001$. Pearson's correlation coefficients and their significance calculated for centroid size and the "ecogeographic" parameters are shown in table 2. Separate analyses for the two species indicate, however, different directions of size change, as the "ecogeographic" vector is positively correlated with latitude in *A. niloticus* (0.99), whereas it has a negative correlation in *A. testicularis* (–0.97). As a result, size decreases southwards in *A. niloticus* and northwards in *A. testicularis.*

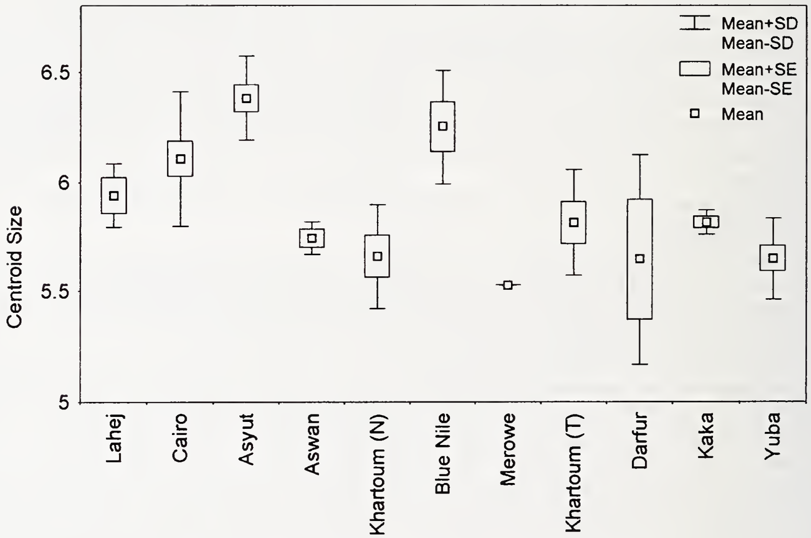

Fig. 3. Box plot of centroid size for the populations.

Analysis of shape differences

Sexual dimorphism in adults was tested through MANOVAs for each landmark, population by population (excluding Merowe, Sherik, and Lahej). Fourteen significant differences were found at $P < 0.05$ (Landmarks 2, 5, 7, 8, 12, 16, 19, 24, and 28 in Cairo; Landmarks 3, 24, and 29 in the Blue Nile; Landmarks 5 and 16 in Kaka; Landmark 15 in Asyut) out of the 203 landmarks tested. This effect was considered negligible and all further analyses were performed irrespective of sex.

Table 2. Relationships of size and shape with ecogeography. Column 2: multiple regression correlation coefficients of centroid size with the "ecogeographic" parameters (* = P < 0.05, ** = P < 0.001). Columns 3 and 4: Partial Least Squares, correlation of the original variables (the principal components from the Procrustes aligned specimens and the "ecogeographic" descriptors) with first shape end "ecogeographic" latent vectors.

	correlation coefficient	shape	ecogeography
Principal component 1		0.95**	0.50**
Principal component 2		0.23*	0.12
Latitude	0.44**	0.53**	0.94**
Longitude	0.05	0.40**	0.03
Mean annual rainfall	–0.12	–0.32*	–0.92**
Mean August rainfall	–0.16	–0.38*	–0.89**
Mean January rainfall	0.21*	0.24*	0.15
Mean annual temperature	–0.47**	–0.46**	–0.68**
Mean August temperature	–0.39**	–0.44**	–0.89**
Mean January temperature	0.08	0.28*	0.67**
Dry days / year	0.09	0.29*	0.87**
Semi-humid days / year	–0.14	–0.37**	–0.83**
Humid days / year	–0.03	–0.19	–0.83**

As shown in figure 4 A, the second principal component clearly represents an explanatory factor of the differences between age classes (the Pearson correlation coefficient is 0.646, P = 0.0001). This vector constitutes 12% of total variance, so it is a relatively important inter-individual variable. Shape differences associated to this second 'growth' vector are illustrated in figure 5 A: adults are characterised by a short rostrum, as well as by a braincase which is short and laterally restricted in correspondence to the sutures of parietals with the frontal bones. The lateral and frontal views of the skull highlight the process of shape change during growth. In fact the braincase profile becomes lower and it is laterally compressed, the orbits move slightly downward and the foramen magnum expands.

The first principal component represents 26% of the total variance and shows differences between populations and species (Fig. 4 A, B). This pattern is not affected by sex, age, and by their interaction, as shown by the model II ANOVA (F values are, respectively: 2.09, 0.90 and 0.79; all not significant).

The scatter plot of principal components one and two in figure 4 A shows the morphometric differences between species. Figure 4 B represents the ordination of population means onto principal component one and three, and suggests an opposite clinal trend in shape, as the scores of *A. testicularis* increase southwards while those of *A. niloticus* increase northwards. The third principal component (7% of total variance) describes differences between populations within *A. niloticus* and *A. testicularis.*

Morphometric relationships based on shape are shown by the Minimum Spanning Tree from the Procrustes distances (Fig. 4 B). Two main clusters are clearly evident, corresponding to the two species. It should be underlined that the Yemenite population of Lahej clusters with *A. niloticus.*

Differences between the two species are shown graphically as shape changes from the consensus in figure 5 B. *A. testicularis* is characterised by a backward shift and expansion of the post-parietal bones, a lowering of the vault, and an upward shift of the foramen magnum. Moreover, zygomatic arches of this species have moved upwards.

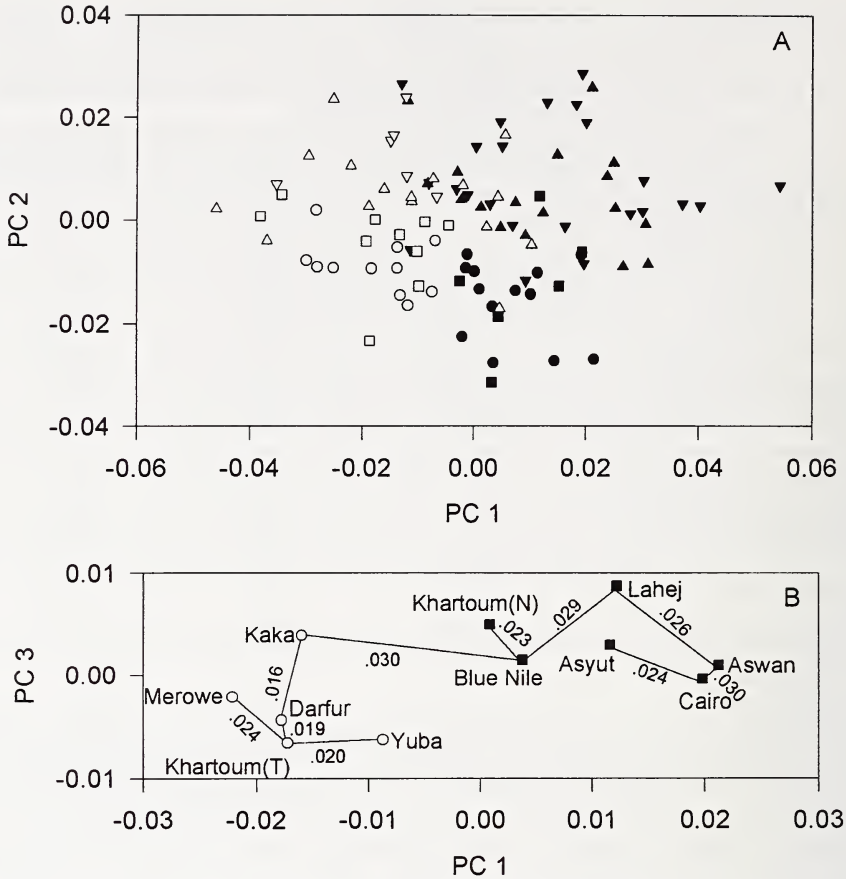

Fig. 4. Principal components analysis of the Procrustes aligned specimens. Part A: Scatter plot of the first two principal components; individuals are shown by age class and species. Circles, age class 1; squares, age class 2; triangles, age class 3; reversed triangles, age class 4; filled symbols are for *A. niloticus* and open symbols for *A. testicularis*. Part B: Scatter plot of first and third principal components, with population means only. A Minimum Spanning Tree is superimposed on the plot; numbers indicate segment lengths.

Partial Least Squares reveal a clear geographic pattern of variation in shape. Correlation between first, second, and third shapes and "ecogeographic" latent vectors are, respectively, 0.53, 0.26, and 0.15. The first shape latent variable is highly correlated to the first principal component computed on the Procrustes aligned specimens, and the first "ecogeographic" vector to latitude, mean annual rainfall, mean August temperature, and number of dry, semi-dry, and rainy days per year (Tab. 2). This first latent vector constitutes 73% of total variance.

Relationships between shape and ecogeography are shown in the scatter plot between first shape and "ecogeographic" vectors (Fig. 6). It suggests a pattern of morphometric variation in shape across populations from North to South. There is a gap at the level of Khartoum, where both species occur. They both have the same score for the first "ecogeographic" vector, but a very different score for the first shape vector. Moreover, separate PLS analyses for the two species show an inverse direction in shape change: scores on the shape latent vector increase from North to South in *A. testicularis* while they diminish in *A. niloticus*.

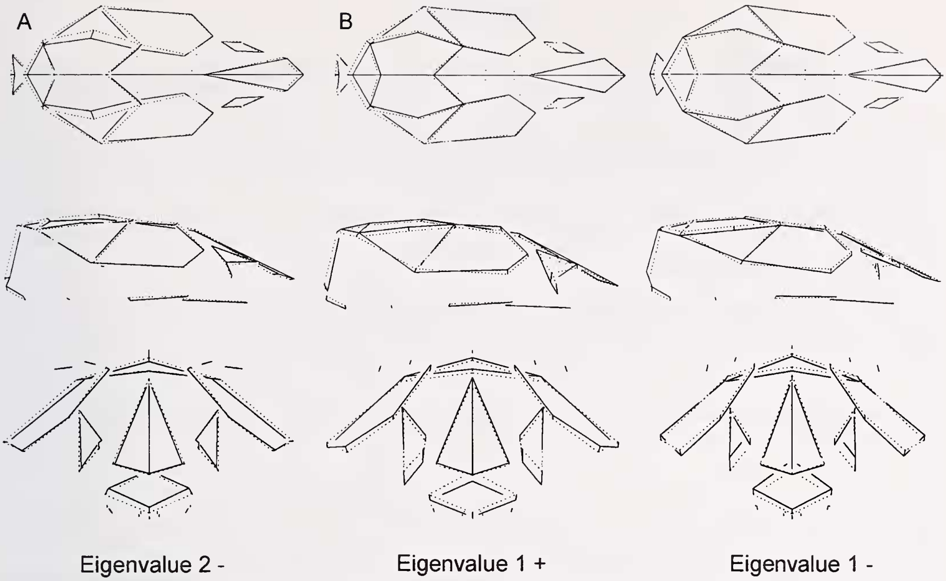

Fig. 5. Shape variation associated with the first two principal components. The dotted lines indicate the shape of the consensus (average), and the solid lines show the kind of shape change relatively to the consensus occurring in the positive (sign plus) and negative (sign minus) directions of eigenvector 1 and 2 (see Fig. 4, for the individual and population scores onto each eigenvector). Part A: Eigenvector 2 shows shape changes occurring from age class 1 (positive scores) to age class 4 (negative scores, the only shape shown). Part B: Eigenvector 1; shape changes from the consensus in *A. niloticus* (plus sign) and *A. testicularis* (minus sign). From top to bottom: upper, lateral, and frontal views of the skull.

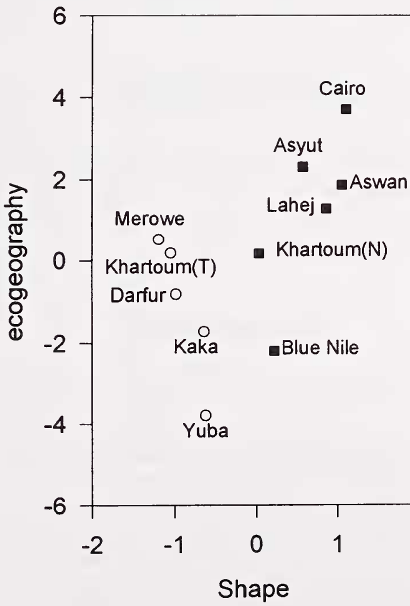

Fig. 6. Scatter plot of Partial Least Square between the first latent shape and "ecogeography" vectors; open circles: *A. testicularis*; filled squares; *A. niloticus* (population means are shown).

Discussion

There are two main points which merit a discussion: differences between age classes and populations, and the origin of morphometric variation across the Nile Valley and its systematics implications.

Pattern of shape changes during growth and of size and shape differences between populations were made possible by the decomposition of the form into its size and shape components. The relevance of shape variation due to different age can lead to misleading interpretations of the results. For this reason, shape variability according to age classes must be taken into account.

As far as the origin of morphometric variation is concerned, results indicate that variation in size and shape is clinal from North to South. This could be due to one lineage whose morphology progressively changes due to natural selection for current conditions, e.g. aridity, or to two separate, morphologically distinct phylogenetic lineages meeting parapatrically and forming a secondary contact area. The first explanation hypothesises an 'ecological cause'; the second a 'phylogenetic cause' (Endler 1986). If the ecological cause is correct, one would expect a continuous correlation from North to South between ecogeography and form. On the contrary, if the 'phylogenetic' explanation is correct, although a correlation between ecogeography and form would be expected in its entirety, there would however be an indication of different patterns within the two taxa.

The results favour the 'phylogenetic' rather than the 'ecological' explanation, both for size and shape variation. Size increases northwards in *A. niloticus* and southwards in *A. testicularis*, and the first shape latent vector is positively correlated with latitude in *A. niloticus*, while is negatively correlated in *A. testicularis*. Moreover, there are evident morphometric differences between populations of the two species occurring in the Khartoum area.

These different clinal patterns in size and shape change would reflect different pathways of range expansion in *A. niloticus* and *A. testicularis*, most probably after the Late Quaternary, when the Nile was a seasonal river (Adamson et al. 1980).

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Zusammenfassung

Geographische Variation von Arvicanthis (Rodentia, Muridae) im Niltal

Größen- und Formunterschiede von Schädeln der Nagergattung *Arvicanthis* wurden in neun Populationen aus dem Niltal (Ägypten und Sudan) und einer aus dem Jemen analysiert. Ein dreidimensionales (x, y, z) Landmarkensystem (Procrustes analysis) wurde benutzt, um die morphometrische Variation in diesen Populationen zu studieren und damit Differenzen zwischen *A. niloticus* und *A. testicularis* und zugrundeliegende Muster der geographischen Variation zu ermitteln. Größen- und Formunterschiede wurden mit geographischen Parametern (Länge, Breite, Niederschlag, Temperatur) korreliert. Die morphometrische Variation spricht dafür, daß in der untersuchten Region zwei Taxa vorkommen und daß deren Variation Anpassungen an die aktuellen Lebensbedingungen reflektiert. Die Analyse zeigt aber auch, daß die Größen- und Formunterschiede von Art zu Art differieren, was auf eine unabhängige Evolution deutet.

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